

The ontogenetic pattern of *Hippopotamus gorgops*
Dietrich, 1928 revealed by a juvenile cranium from
the one-million-years-old paleoanthropological
site of Buia (Eritrea)

Bienvenido MARTÍNEZ-NAVARRO, Luca PANDOLFI,
Tsegai MEDIN, Yosief LIBSEKAL, Massimiliano GHINASSI,
Mauro PAPINI & Lorenzo ROOK



DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Bruno David, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF : Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR : Adenise Lopes (Académie des sciences ; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT : Fariza Sissi (Muséum national d'Histoire naturelle ; fariza.sissi@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS : Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, *took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article*) :

Micropaléontologie/*Micropalaeontology*

Maria Rose Petrizzo (Università di Milano, Milano)

Paléobotanique/*Palaeobotany*

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/*Metazoa*

Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléochthyologie/*Palaeoichthyology*

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*

Juliana Sterli (CONICET, Museo Paleontológico Egidio Feruglio, Trelew)

Lépidosauromorphes/*Lepidosauromorphs*

Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*

Eric Buffetaut (CNRS, École Normale Supérieure, Paris)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*

Lorenzo Rook (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*

Roberto Macchiarelli* (Université de Poitiers, Poitiers)

Archéologie préhistorique/*Prehistoric archaeology*

Marcel Otte (Université de Liège, Liège)

RÉFÉRÉS / REVIEWERS : <https://sciencepress.mnhn.fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER :

Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol is indexed by*:

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par / *Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on*:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publishes*:

Adansonia, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes*:

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)
ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

The ontogenetic pattern of *Hippopotamus gorgops* Dietrich, 1928 revealed by a juvenile cranium from the one-million-years-old paleoanthropological site of Buia (Eritrea)

Bienvenido MARTÍNEZ-NAVARRO

IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social,
C/ Marcel·lí Domingo s/n, Campus Sescelades, Edifici W3 43007 Tarragona (Spain)
and Area de Prehistoria, Universitat Rovira i Virgili (URV),
Avda. Catalunya 35, 43002 Tarragona (Spain)
and ICREA, Pg. Lluís Companys 23 08010 Barcelona (Spain)
bienvenido.martinez@icrea.cat (corresponding author)

Luca PANDOLFI

Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira, 4 50121 Firenze (Italy)

Tsegai MEDIN

IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/ Marcel·lí Domingo s/n,
Campus Sescelades, Edifici W3 43007 Tarragona (Spain)
and Commission of Culture and Sports (Eritrea), Po.Box. 1500, Asmara (Eritrea)

Yosief LIBSEKAL

National Museum of Eritrea, P.O.Box 5284, Asmara (Eritrea)

Massimiliano GHINASSI

Dipartimento di Geoscienze, Università di Padova, via Giotto 1 35137 Padova (Italy)

Mauro PAPINI

Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira, 4 50121 Firenze (Italy)

Lorenzo ROOK

Dipartimento di Scienze della Terra, Università di Firenze, via G. La Pira, 4 50121 Firenze (Italy)

Submitted on 22 January 2020 | Accepted on 8 August 2020 | Published on 22 February 2022

[urn:lsid:zoobank.org:pub:44C3C4F7-9FC6-41CE-BA6F-9FCDA4F25462](https://zoobank.org/pub:44C3C4F7-9FC6-41CE-BA6F-9FCDA4F25462)

Martínez-Navarro B., Pandolfi L., Medin T., Libsekal Y., Ghinassi M., Papini M. & Rook L. 2022. — The ontogenetic pattern of *Hippopotamus gorgops* Dietrich, 1928 revealed by a juvenile cranium from the one-million-years-old paleoanthropological site of Buia (Eritrea). *Comptes Rendus Palevol* 21 (7): 157–173. <https://doi.org/10.5852/cr-palevol2022v21a7>

ABSTRACT

An almost complete cranium of a juvenile individual from the late Early Pleistocene site of Buia, in the northern Afar (Danakil) Basin in Eritrea, reveals a different growth pattern of the extinct species *Hippopotamus gorgops* Dietrich, 1928 compared to the extant species *Hippopotamus amphibius* Linnaeus, 1758. The specimen shows important cranial features of *Hip. gorgops* (also visible in adult

KEY WORDS

Juvenile, ontogeny, geometric morphometrics, Danakil depression, Buia, Eritrea.

specimens), with a derived cranial anatomy that is related to the specialization to a more aquatic life style than other species of Hippopotamidae: elevated nuchal and sagittal crests, strongly elevated orbital cavities, short neurocranium and elongated palate. A geometric morphometrics analysis was performed in the lateral view on skulls of *Hip. gorgops* and *Hip. amphibius*, to investigate size-shape relationship and to compare ontogenetic growth trajectories between both taxa. The study revealed that, during growth (increase in size and age), variations in skull shape are prominent in *Hip. amphibius*; juvenile and adult individuals of *Hip. gorgops* display strong morphological similarities but size and shape are poorly correlated. The results support the hypothesis that in a relatively early ontogenetic stage, *Hip. gorgops* was more specialized in its aquatic adaptation than *Hip. amphibius*.

RÉSUMÉ

Modèle ontogénétique d'Hippopotamus gorgops Dietrich, 1928 révélé par un crâne juvénile du site paléanthropologique de Buia (Érythrée) daté d'un million d'années.

Un mode de croissance dans l'ontogenèse de l'espèce éteinte *Hippopotamus gorgops* Dietrich, 1928, différent de celui de l'espèce actuelle *Hippopotamus amphibius* Linnaeus, 1758, est révélé par un crâne presque complet d'un individu relativement juvénile en provenance du site paléanthropologique du Pléistocène inférieur final de Buia, dans au nord du bassin Afar (Danakil), en Érythrée. Ce spécimen montre certaines des caractéristiques crâniennes les plus importantes de *Hip. gorgops* (comme on le voit sur les spécimens adultes), avec une anatomie crânienne dérivée qui est liée à la spécialisation à un habitat plus aquatique que les autres espèces de ce clade : crêtes nucales et sagittales élevées, cavités orbitales très élevées, neurocrâne court et museau allongé. Une analyse de morphométrie géométrique a également été réalisée en vue latérale sur des crânes de *Hip. gorgops* et *Hip. amphibius*, afin d'étudier la relation taille-forme et de comparer les trajectoires ontogénétiques de croissance entre les deux taxons. L'étude a révélé que, pendant la croissance (augmentation de la taille et de l'âge), les variations de forme du crâne sont importantes chez *Hip. amphibius*, tandis que les individus juvéniles et adultes de *Hip. gorgops* présentent de fortes similitudes morphologiques, alors que la taille et la forme sont mal corrélées. Les résultats confirment l'hypothèse qu'à un stade ontogénétique relativement précoce, *Hip. gorgops* était plus spécialisé à son habitat aquatique que *Hip. amphibius*.

MOTS CLÉS

Juvenile, ontogénie, morphométrie géométrique, dépression de Danakil, Buia, Érythrée.

INTRODUCTION

The fossiliferous area of Buia (100 km south of Massawa, northern Danakil Depression, Eritrea) (Fig. 1) was discovered in 1995 during a preliminary geological survey under the aegis of a collaborative research program between the Department of Mines (Eritrean Ministry for Energy and Water Resources, Asmara) and the Department of Earth Sciences of the University of Florence. Studies were carried out in the area during several field seasons in 1995-1997 and 2003-2004, also involving research teams from the National Museum of Eritrea as well as other Italian and European institutions.

These activities led to the discovery of a new important paleoanthropological site at Buia (Abbate *et al.* 1998; Rook *et al.* 2002; Zanolli *et al.* 2014), where an abundant fossil vertebrate collection was recovered (Ferretti *et al.* 2003; Delfino *et al.* 2004, 2018; Martínez-Navarro *et al.* 2004b, 2010; Rook *et al.* 2010, 2013; Medin *et al.* 2015). A large number of archaeological localities with extraordinarily abundant and well-preserved Mode 1 (Oldowan) and Mode 2 (Acheulean) tool industries (Martini *et al.* 2004) were also identified in this area.

The chronology of the site has been established at around 1.0 Ma, inside the normal subchron Jaramillo by paleomagnetism analysis (Abbate *et al.* 1998; Albanielli & Napoleone 2004; Ghinassi *et al.* 2015) coupled with mammal biochronology (Ferretti *et al.* 2003; Martínez-Navarro *et al.* 2004b), and

fission-track dating (Bigazzi *et al.* 2004). Most of the information from the site is included in the monographic volume entitled "A step towards human origins: The Buia *Homo* one-million-years ago in the Eritrean Danakil Depression (East Africa)" edited by Abbate *et al.* (2004a), as well as in recent reviews of the detailed stratigraphy, sedimentology, tectonics, and geological mapping of the area (Ghinassi *et al.* 2009, 2013, 2015; Papini *et al.* 2014; Sani *et al.* 2017; Scarciglia *et al.* 2018).

Hippopotamids are the most abundant large mammals at the Buia site (see Martínez-Navarro *et al.* 2004b), and they also dominate many other eastern African Plio-Pleistocene assemblages (see Coryndon 1976; Géze 1980, 1985; Harris *et al.* 1988; Harris 1991; Boisserie 2002, 2005). At Buia, two species have been reported (Martínez-Navarro *et al.* 2004b): *Hippopotamus gorgops* and *Hexaprotodon* sp. (preliminarily referred to *Hexaprotodon karumensis* Coryndon, 1977 in Abbate *et al.* 1998). The latter corresponds to a small-sized hippopotamid lineage, relatively common in the eastern African assemblages, but rare in the Pleistocene of the Afar region. Its description is based on few postcranial elements, especially on the left talus (MHB 5) and on the right magnum (DAN 246) (see Martínez-Navarro *et al.* 2004b: fig. 7).

The last occurrence of small-sized (not insular) hippopotamids in the Afar region is seen in the recently described species *Hexaprotodon bruneti* (Boisserie & White, 2004) from Maka and Bouri Peninsula (Ethiopia). It is found in a chronology

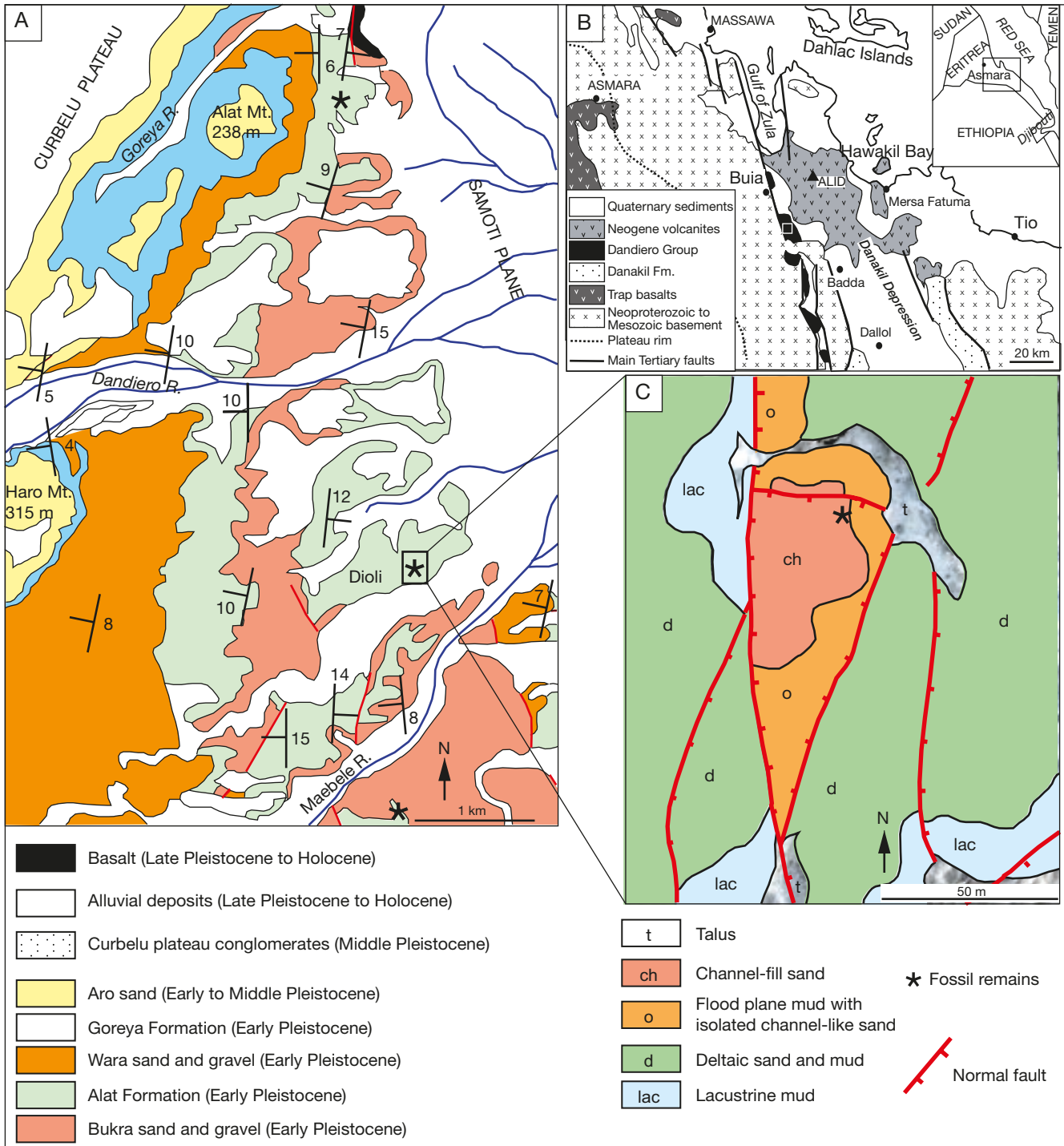


FIG. 1. — **A**, Location of the study area on a regional geologic scheme of Eritrea; **B**, geological map of the Buia Basin with location of the fossiliferous sites mentioned in the text; **C**, detail on the geological features of the locality where the cranium of juvenile *Hippopotamus gorgops* Dietrich, 1928 was found.

around 2.5 Ma and characterizes the Pliocene/Pleistocene transition (fixed at 2.588 Ma by the International Commission on Stratigraphy). *Hexaprotodon bruneti* is possibly an immigrant that would belong to the well-known clade of Asian origin of which *Hexaprotodon sivalensis* Falconer & Cautley, 1836 from the Siwaliks is the representative species. Along with another late Miocene hippopotamid from Toros-Ménalla in Chad, *Hex. bruneti* from the Afar region is the only species of

the genus *Hexaprotodon* in Africa (Boisserie & White 2004; Boisserie *et al.* 2005). This Asian genus has no continuity during the Pleistocene in the Afar region or elsewhere in the continent (Boisserie 2005).

This clade is different to all the other small-sized continental African hippopotamids, which have an African origin and evolution. It does not fit the diagnosis of the genus *Hippopotamus*. Then, it is included, until it is described, in an undetermined

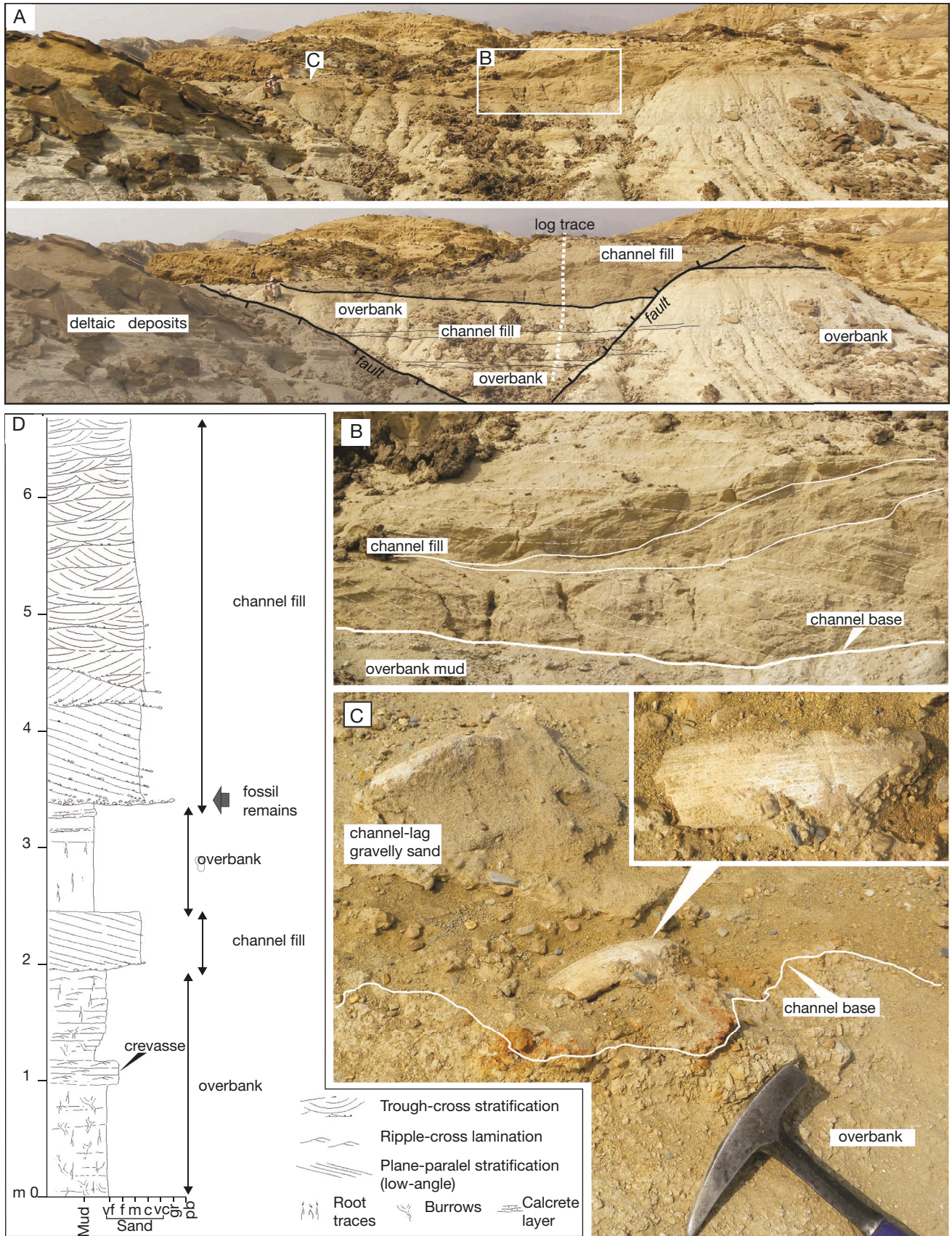


FIG. 2. — Sedimentary and stratigraphic features of the Dioli “A037” study site: **A**, panoramic view of the site and relative stratigraphic interpretation; **B**, close view of the sandy channel-fill deposit forming the upper part of the hill; **C**, a canine of *Hippopotamus* outcropping in the gravelly sand channel-lag deposits; **D**, sedimentological log across the study site. Note the location of fossil specimen at the base of channel-fill deposits. Photos: **A-C**, taken in November 2010.

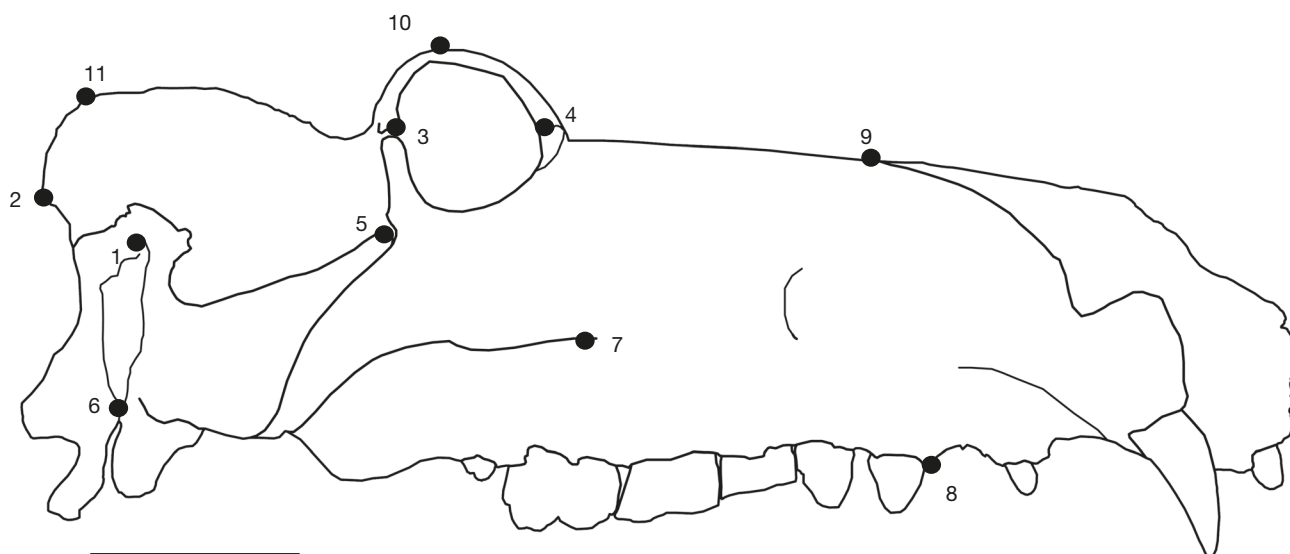


FIG. 3. — Landmark configuration of *Hippopotamus* Linnaeus, 1758 skull in lateral (mostly derived from van der Geer *et al.* 2018): 1, parietal-temporal-occipital suture; 2, posterior border of the nuchal crest; 3, tip of postorbital process; 4, lacrimal; 5, anterior projection of zygomatic process of temporal bone; 6, mastoid process; 7, joint point between zygomatic arch and maxilla; 8, the most anterior element of the premolar series; 9, posterior point of incisive at the incisive maxilla suture; 10, top of the orbit; 11, top of the nuchal crest. Scale bar: 10 cm.

genus called aff. *Hippopotamus* (Boisserie 2005), together with the species aff. *Hippopotamus karumensis*, a particularly large species, and aff. *Hip. aethiopicus*.

In accordance with Boisserie (2005), we consider that the small-sized continental form of hippopotamid from Buia cannot be included in the genus *Hexaprotodon*, which is largely of Asian origin, and probably it has to be included in the still undescribed taxon of eastern African origin aff. *Hippopotamus*.

In this research, we concentrate the study on a mostly complete cranium of a juvenile individual of the largest species of hippo, *Hippopotamus gorgops*, which is a common taxon in Africa well documented in several localities of the Turkana Basin (where it is reported from the Plio-Pleistocene transition to the early middle Pleistocene: Dietrich 1926, 1928; Harris 1991; Weston & Boisserie 2010), in the Western Rift (Faure 1994; Weston & Boisserie 2010) as well as in the middle Pleistocene of South Africa (Cornelia: Hooijer 1958) and, outside Africa, in the early Pleistocene of the Near East (Ubeidiya in Israel; Faure 1986).

Here, we present a geometric morphometrics comparative study performed in order to investigate size-shape relationship between *Hip. gorgops* and *Hip. amphibius* and to compare variations in skull shape between the two taxa during the considered ontogenetic stages.

THE JUVENILE *HIPPOPOTAMUS GORGOPS* CRANIAL SPECIMEN DAN-213

GEOLOGICAL SETTING AND STRATIGRAPHIC FRAME OF THE LOCALITY A037

The juvenile cranial specimen DAN 213 was found at locality A037 (Buia Project site code); UMTS coordinates 37P

E601107 N1628110; Buia basin, south of Dandero river, Danakil depression, Eritrea (Fig. 1). It comes from the upper part of a small hill located in the central part of the Dandero Basin (Abbate *et al.* 2004a; Papini *et al.* 2014), about 100 km south of the Gulf of Zula (Fig. 1A).

The Dandero Basin succession consists of three unconformity bounded units: Maebele Synthem, Curbelu Synthem and Samoti Synthem. The Maebele Synthem (about 300–400 m thick) contains six lithostratigraphic units, from bottom to the top (Fig. 1B): fluvial Bukra sand and gravels, fluvio-deltaic Aalat Formation, fluvial Wara Sand and Gravel, lacustrine Goreya Formation, fluvio-deltaic Aro Sand and alluvial fan Addai Fanglomerate. The sand and silt alluvial deposits forming the site that provided the juvenile cranium of *Hippopotamus gorgops* belong to the fluvio-deltaic Aalat Formation (Ghinassi *et al.* 2009; 2015), which was accumulated almost during the Jaramillo Subchron (Abbate *et al.* 2004b; Ghinassi *et al.* 2015).

The sedimentary succession exposed in the surroundings of the study site is affected by numerous E-W trending normal faults (Fig. 2A), which hinder a detailed correlation of the stratigraphic surface over long distances. The study hill is made of two parts separated by an E-W trending fault. The southern part consists of barren silty sand deltaic deposits (Fig. 2), whereas the northern part is formed by fossil-rich alluvial sand and silt. In particular, two main intervals can be distinguished in this northern part (Fig. 2A, D). The lower interval is made of massive, bioturbated mud, which bears evidence of intense pedogenesis. Tabular beds of fine to medium sand (3–15 cm thick) are interbedded within the mud. These layers are commonly massive because of intense pedogenesis, although faint of ripple-cross lamination can be locally distinguished. Lensoid bodies with erosive, concave upward base and flat top (0.3–0.5 m thick and 5–10 m wide)

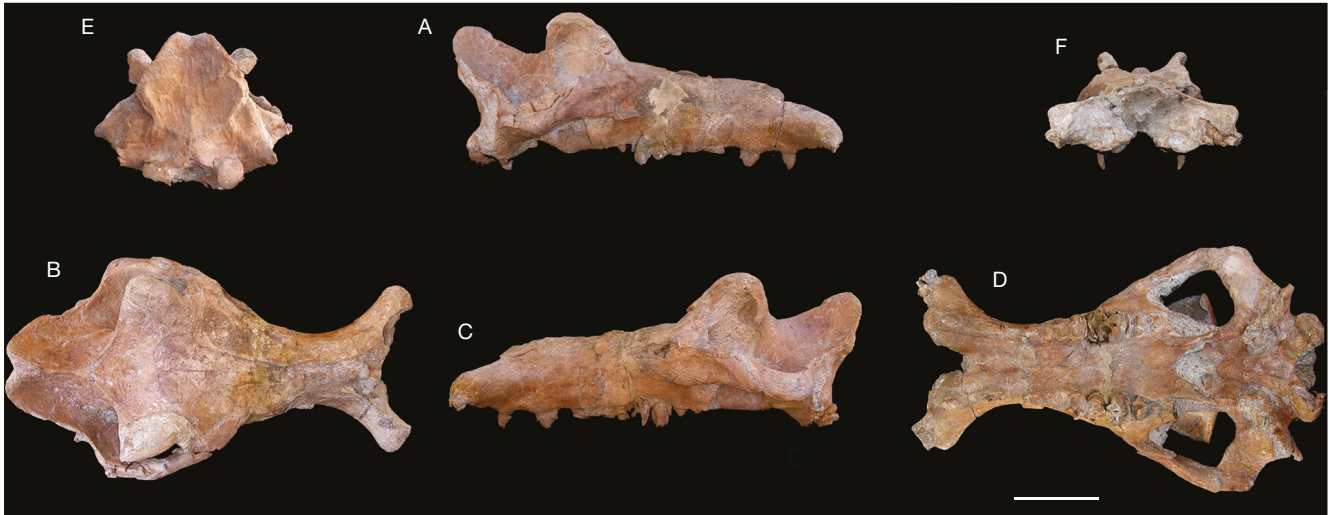


FIG. 4. — Cranium DAN-213 from Dioli, juvenile specimen of *Hippopotamus gorgops* Dietrich, 1928: **A**, right lateral view; **B**, upper view; **C**, left lateral view; **D**, lower view; **E**, posterior view; **F**, anterior view. Scale bar: 10 cm.

can be locally present. These bodies show a fining upward trend, from medium to fine sand and are commonly characterized by a low-angle (10-15°) cross stratification. Sedimentary feature of these deposits are indicative of an alluvial-plain setting (Bridge 2003), where sand transport in isolated channels gave rise to the lensoid sedimentary bodies. In this frame, episodic flood events allowed spreading of the sandy bedload onto the overbank areas, giving rise to the tabular sandy beds (i.e., Willis & Behrensmeyer 1994; Ghinassi *et al.* 2005). Mud sedimentation occurred in ephemeral ponds developed after the main flood events. The upper part of the hill consists of well-stratified sandy deposits overlaying a markedly erosive surface cutting the muddy overbank of the lower interval. Such an erosive surface is floored by pebble-rich, coarse sand, which provided abundant fossil bones (Fig. 2C), including the specimens showed in this study. The overlying sandy deposits are mainly made of plane-parallel and trough-cross stratified beds up to 80 cm thick (Fig. 3D). These beds are 10°-20° inclined (Fig. 2B), and their dip is commonly transverse to the main palaeoflow documented by cross-stratification. These sandy deposits were accumulated in a fluvial channel setting as sandy channel bars (Bridge 2003). The basal fossil-rich sandy interval is interpreted as channel lag (Fidolini *et al.* 2013), which was formed by accumulation of the coarser particles under tractional conditions.

As attested in previous papers (Martínez-Navarro *et al.* 2004b), fossil remains ascribed to *Hippopotamus gorgops* are found at other localities of the Buia Basin. Specimens from the area of A037 site (south of Dandero river) are labeled as DAN#, while those coming from the Wadi Aalad hominin site (37P E600710 N1632638) are labeled as UA#; finally, specimens labeled as MHB#, comes from site N277 (37P E601527 N1623811), south of Mahabale stream (Fig. 1A, B). The three sites are correlated on the basis of lithostratigraphy (Aalat Fmt.); Dioli A037 and Wadi Aalad *Homo* site are also correlated on the basis of their paleomagnetic signature.

GEOMETRIC MORPHOMETRICS AND ALLOMETRY

Material

We collected images from 42 skulls of *Hippopotamus* (39 *Hip. amphibius*, 3 *Hip. gorgops*) in lateral view, mainly from original photos (Appendix 1). The lateral view better describes variation in shape of skull within Hippopotamidae and their specialization to different life-styles (Pandolfi *et al.* 2020). Fossil *Hip. gorgops* is poorly represented by complete skulls, and juvenile individuals have been never described before this work. Thus, the specimen here reported represents an important contribution to increase the available dataset and to compare allometry between the two considered taxa. The dataset of *Hip. amphibius* includes a representative sample (39 specimens) with adult and juvenile individuals, mainly from the Congo river (Appendices) and housed at Royal Museum for Central Africa (RMCA), in Bruxelles. Appendices reports the specimen list, the number of individuals for each species, the estimated age-group as well as the list of institutions from which the images used for shape acquisition were collected. In addition, the values of PCs and Centroid Size are also reported for each specimen in order to provide a comparative sample that could be used for additional analyses.

Relatively class age has been calculated for each specimen, following dental eruption pattern. We used the class ages reported by Laws (1968); thus, we estimated the class age for each skull with associated mandible. Due to collection management or sample collection, some skulls were provided without relative mandibles. In this case we estimated the class age by comparing the upper teeth eruption and wear with aged skulls. Finally, we considered the skulls with fully erupted and worn M3s (from 15 to 19 in Laws 1968) as belonging to the same group of adults (Class 15; Appendices). Images of upper tooth series for each considered class age are reported in the Appendix 2.

Methods

We digitized 11 homologous anatomical landmarks in lateral view on each specimen (Fig. 3), using the tpsDig2 v2.17

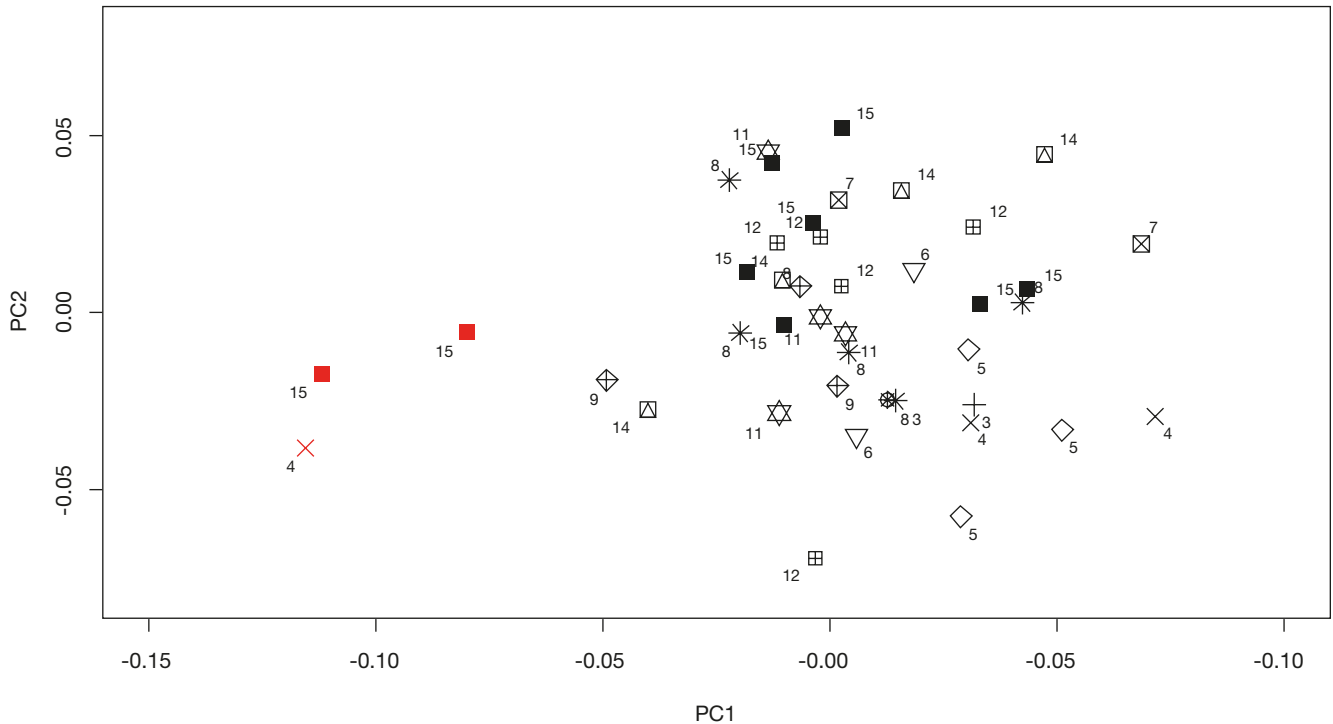


FIG. 5. — Scatterplot between PC1 and PC2 of the considered *Hippopotamus* skulls in lateral view. Species: **red points**, *Hippopotamus gorgops* Dietrich, 1928; **black points**, *Hippopotamus amphibius* Linnaeus, 1758. Numbers on plotted points and symbols refer to relative ontogenetic class age. **Plus**, class 3; **cross**, class 4; **diamond**, class 5; **triangle point down**, class 6; **square cross**, class 7; **star**, class 8; **diamond plus**, class 9; **triangles up and down**, class 11; **square plus**, class 12; **square and triangle**, class 14; **filled square**, class 15. (see Methods and Appendices).

software (Rohlf 2013). Rostral region is often damaged, or entirely lacking, therefore it is excluded from the shape configuration. We followed the protocols of Marcus *et al.* (2000) and Mullin & Taylor (2002) to minimize parallax and measurement error on the photographs. Scale bars were used to scale each digitized specimen. In order to eliminate inter-observer error, the same operator (L.P.) digitized the entire landmark dataset. All the analyses have been performed in R workspace. Generalized Procrustes Analysis (GPA) (Bookstein 1986; Goodall 1991), implemented in the `procSym()` function from the R-package “Morpho” (Schlager 2014), was used to rotate, translate and scale landmark configurations to unit centroid size (CS: the square root of the sum of squared distances of the landmarks from their centroid) (Bookstein 1991). After GPA, a Principal Components Analysis (PCA) was performed in order to visualize orthogonal axes of morphological variation. Centroid size (CS: the square root of the sum of squared Euclidean distances from each landmark to their centroid; see below) is used as a measure of overall skull size. In order to visualize shape changes in ordination plots we adopted the method described in Márquez *et al.* (2012). Relationship between shape and size has been investigated following the method proposed by Mitteroecker *et al.* (2004). Procrustes shape variables have been decomposed into a CAC (common allometric component, which is the scaled vector of regression slopes estimated using a pooled regression of the shape variables on the log centroid size) and a RSC1 (first residual shape

component, which describes the nonallometric component and is the PC1 scores of the residuals of the pooled regression analysis) (see Mitteroecker *et al.* 2004; Aristide *et al.* 2019). The two new variables have been plotted for each considered specimen. Relationship between allometric shape and size has been also investigated plotting the CAC value and the CS. Correlations have been tested using the functions `lm()`, `cor.test()` and `adonis()`.

Abbreviations

CAC	Common allometric component;
CS	Centroid size;
GPA	Generalized Procrustes Analysis;
PCA	Principal Components Analysis;
RSC1	First residual shape component.

MORPHOLOGICAL DESCRIPTION AND COMPARISONS OF THE JUVENILE CRANIAL SPECIMEN DAN-213

Specimen DAN-213 is an almost complete cranium (Fig. 4). Biometric data of the specimen are provided in Table 1. As all the other specimens from the Buia site collection, it is housed at the National Museum of Eritrea (Asmara, Eritrea).

It was found in two different pieces at the same site by one of us (LR), the nasal and palate region in the 1997 season, and the neurocranium in the 2004 season. After preparation and cleaning of both specimens, they fit perfectly together along a

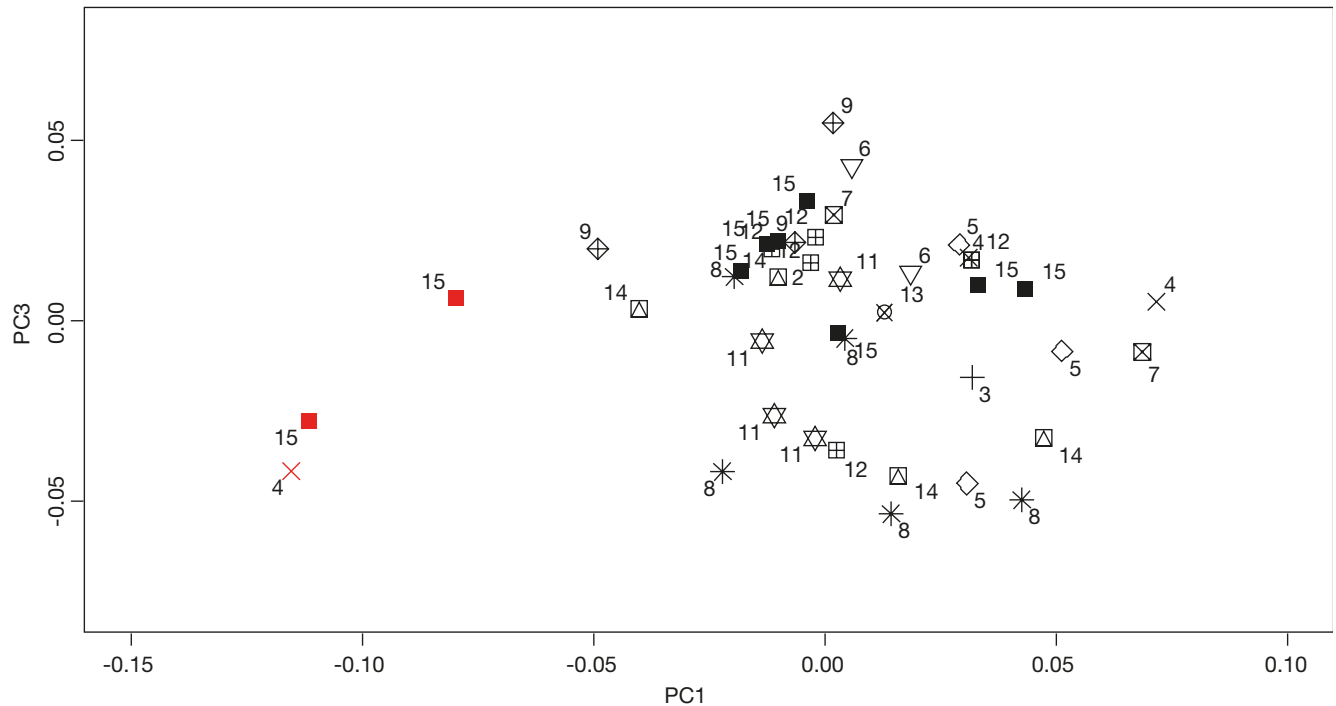


FIG. 6. — Scatterplot between PC1 and PC3 of the considered *Hippopotamus* skulls in lateral view. Species: **red points**, *Hippopotamus gorgops* Dietrich, 1928; **black points**, *Hippopotamus amphibius* Linnaeus, 1758. Numbers on plotted points and symbols refer to relative ontogenetic class age. **Plus**, class 3; **cross**, class 4; **diamond**, class 5; **triangle point down**, class 6; **square cross**, class 7; **star**, class 8; **diamond plus**, class 9; **triangles up and down**, class 11; **square plus**, class 12; **square and triangle**, class 14; **filled square**, class 15. (see Methods and Appendices).

para-coronal plane fracture at the level of mid/M¹s and there is no doubt that they belong to the same individual (Fig. 4).

Although juvenile, the specimen represents a large sized individual. The neurocranium is high and antero-posteriorly shortened as it is in the adult individuals of *Hip. gorgops* and the European species *Hip. antiquus* (Mazza 1991; Martínez-Navarro *et al.* 2015; Pandolfi & Petronio 2015; Pandolfi *et al.* 2020); nuchal and sagittal crests oriented backward; pronounced temporal crests; occipital transversely narrow and high, with the occipital condyles slightly more prominent than in the juveniles of similar age in the extant species *Hip. amphibius*; lacrimal bones connected with the nasals; nasals extend to the posterior levels of the orbits; basioccipital thick at the posterior tuberosities and thin at the anterior ones; mastoideus and paraoccipital processes well marked; zygomatic arches antero-posteriorly elongated and medio-laterally compressed; orbital cavities very elevated, periscopic, more than in *Hip. amphibius*, as in the adults of *Hip. gorgops* and *Hip. antiquus*, which also have similar anatomy in the sagittal and nuchal crests; nasal region low and palate proportionately much more elongated than in juveniles of *Hip. amphibius*, with the maximum compression at the diastema between the P² and the DP³; infraorbital foramen very small and situated above the DP³. Unfortunately, the premaxillary bone is not preserved and neither the upper incisors (nor alveoli) are present, but the left and right C, P¹, P², DP³, DP⁴, M¹, and erupting M² are all in position. A peculiar characteristic of the specimen is the occurrence of a large diastema between the P¹ and P², and especially between the P² and DP³.

DENTITION

Canines

It is not clear if they are deciduous or adult canines. Although they are small and show a deep and marked posterior groove, probably they correspond to the apical region of the adult canines, that normally in the extant species *H. amphibius* born at a very juvenile age, in between one and three years old (Laws 1968).

Premolars

P¹s are caniniform with a single cusp and absence of cingulum, placed approximately halfway between the likely position of the incisors and the second premolars; P²s have a single main cusp, with a strong posterior cingulum and a thin labial one. They have a crest orientated diagonally (mesiolingually-distolabially). DP³s are bilobed, deeply worn and badly preserved. DP⁴s are, also, deeply worn, bilobed, with a marked cingulum in the labial face and a very small one (or practically absent) on the lingual face, and with the bucco-lingual diameter of the mesial lobe smaller than the distal one.

Molars

M¹s show their mesial lobe is relatively worn out, and the distal one in the first face of worn (see class ages in Appendix 2), both (right and left) are damaged because of the fracture of the cranium in two parts running on a para-coronal plane at the level of mid/M¹s, the molars are clearly not brachydont, and possess a small posterior cingulum and a thin lingual cingulum; M²s are still erupting from their alveoli.

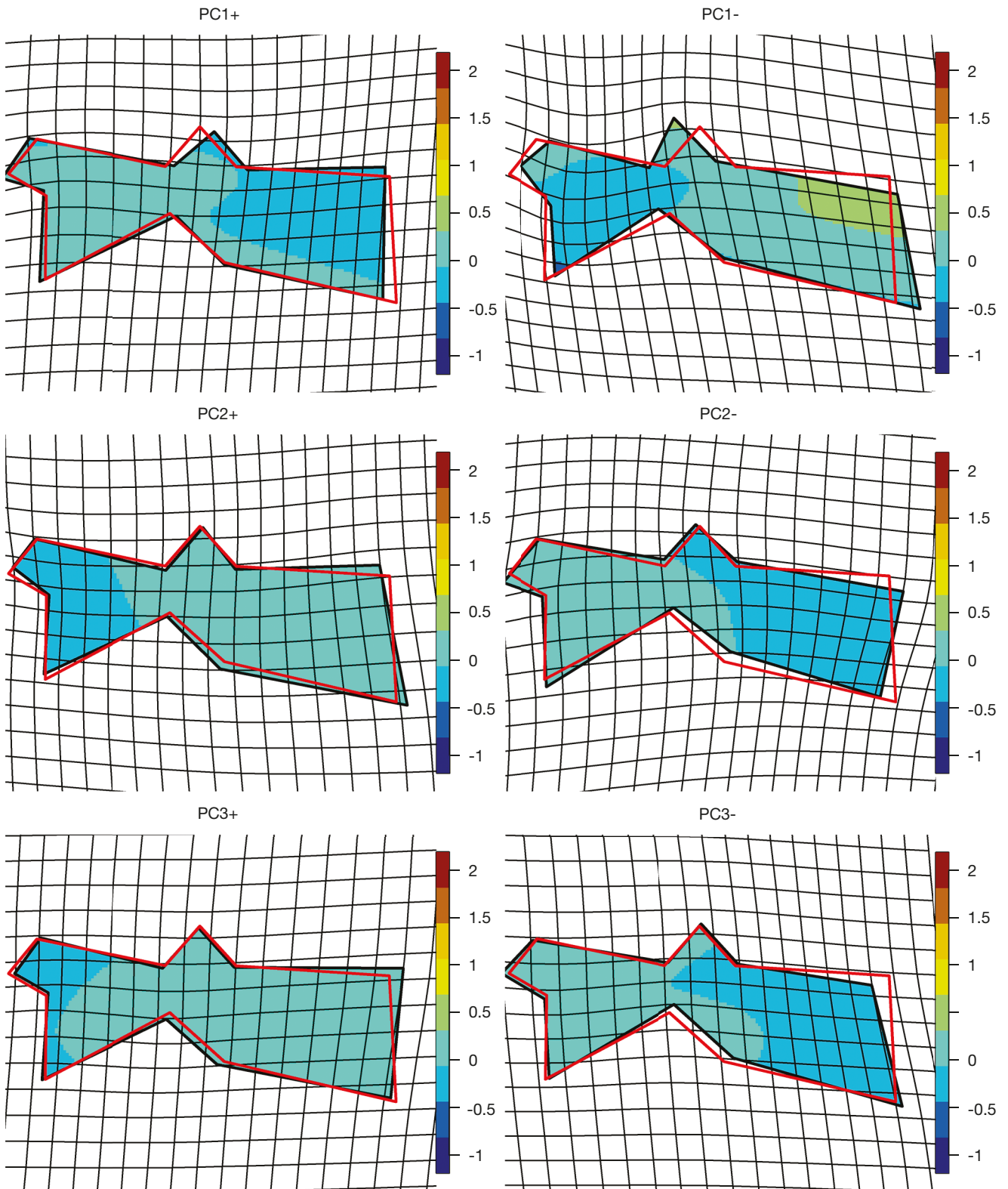


FIG. 7. — Deformation grids refer to the first three PC axis extremes (+, positive, and -, negative) in Figures 5 and 6. Values < 0 indicate that, with respect to the source (here the sample' consensus), the target (here the PC's extremes) experiences a reduction in the local area, while values > 0 indicate an enlargement.

TABLE 1. — Measurements of the juvenile specimen of *Hippopotamus gorgops* Dietrich, 1928 from Buia, DAN 213 (in mm, Following Harris 1991).

Maximum length of the cranium	595
Length C-occipital condyle	500
Length DP1 to occipital condyle	475
Length DP2 to occipital condyle	420
Length post orbital process-occipital condyle	140
Length DP3 to postorbital process	320
Width at the canines	230
Width at infraorbital foramen	–
Maximum width at orbits	230
Minimum width at orbits	170
Width at mastoid	140
Height of the occiput	160 (from top of foramen magnum)
Height of the occiput	210 (from base of condyles)
Width foramen magnum	58.95
Height foramen magnum	49.0
Width occipital condyles	140
Width palate at DP3 (ext)	105
Width palate at M2 (ext.)	136
Width zygoma	310
Dental measurements	Left Right
C	L (medio-lateral) 31.5 33.0
	W (dorso-ventral) 25.0 23.0
P1	L 21.5 22.9
	W 13.4 15.0
P2	L 30.4 30.3
	W 19.0 (17.0)
DP3	L 40.9 (38.0)
	W 26.0 –
DP4	L 42.6 44.0
	Want 28.8 –
	Wpost 35.9 37.0
M1	L 54.1 53.4
	Want 40.1 39.7
	Wpost 43.8 41.5
M2	L (>45) –

The ontogenetic age of the individual is difficult to calculate. It has been compared with the groups of age described by Laws (1968), showing that based on the presence of the adult canine, first and second premolars, the deciduous third and fourth, the stage of wear of the first molar, and the stage of eruption of the second molar, it is in a phase close to the group VI, in an approximate age around 7 ± 1 years old.

GEOMETRIC MORPHOMETRICS

Principal Component Analysis

The first three principal components of the PCA, performed on the skulls in lateral view, summarize 59.77% of total shape variance. Figure 5 shows the relationship between PC1 (29.15% of the total shape variance explained) and PC2 (17.16% of the total shape variance). Figure 6 shows the relationship between PC1 and PC3 (13.56% of the total variance).

Positive PC1 values are associated with low nuchal crest, long neurocranium, massive anterior portion of the skull, relatively low orbit (Fig. 7). Negative PC1 values are associated with a relatively shorter neurocranium, longer anterior portion of the skull, and more elevated orbit. This shape corresponds to *Hip. gorgops*-morphology (Figs 5; 6).

At positive PC2 values the anterior portion of the skull is low, the neurocranial portion is large (Fig. 5). At negative PC2 values the anterior portion of the skull is higher, the zygomatic arch is placed lower (Fig. 5).

Specimens belonging to *Hip. amphibius* are mainly placed at the center of the PC1-PC2 morphospace (Fig. 5).

The skulls belonging to *Hip. gorgops* are located within the fourth quarter of the morphospace and the three specimens are very close to each other (Fig. 5).

The two taxa are located in different areas of the morphospace and this is also evident in the interactive 3d plot reported in the Appendix 3.

Allometry

Figure 8 plots the common allometric component (CAC) and the centroid size for each specimen. In *Hip. amphibius*, CAC score and CS are strictly related (standard linear regression is significant, p -value = $2.625e-08$), and an increase in CS corresponds to an increase in CAC score (correlation coefficient performed with function ‘cor.test’ revealed a value of 0.756) (Fig. 8). This pattern is not evident in *Hip. gorgops* where juvenile specimen, with low CS value, approximates the CAC values of the two adult individuals (Fig. 8).

A similar result can be observed plotting CAC values and RSC1 (Fig. 9).

The shape of the skull in *Hip. gorgops* does not reveal a significant variation from juvenile to adult individuals, whereas, increasing in age, the skull of *Hip. amphibius* increase in size and changes in shape for the chosen configuration. The correlation between shape and size in *Hip. amphibius* is highly significant (p -value = 0.001 using the function `adonis()`).

Unfortunately, the sample size for *Hip. gorgops* is too small to test all these relationships.

DISCUSSION

This is, at best of our knowledge, the most complete and magnificently preserved cranial specimen of a juvenile *Hippopotamus gorgops* described so far in the fossil record. The lack of comparative juvenile specimens makes a species attribution of the fossil difficult the identification of this fossil, because anatomical characteristics of juvenile individuals are not well known.

The new specimen offers important morphological details on the juvenile anatomy of *Hip. gorgops* at the age of around 7 ± 1 years of age, showing that the most significant cranial anatomical derivation of this species occurred from a relatively early ontogenetic stage (see Fig. 4), in comparison to the extant species *Hip. amphibius* (Weston 2003), such as represented in the juvenile specimen AMNH 54248, housed at the American Museum of Natural History in New York, of an ontogenetic age around 11 years (see Fig. 10), and other specimens used in this study. This ontogenetic pattern is evident in the results of the GM study (Figs 5-9). Although the available data are not enough to exhaustively investigate the allometric trajectories within *H. gorgops*, the work represents the first contribution

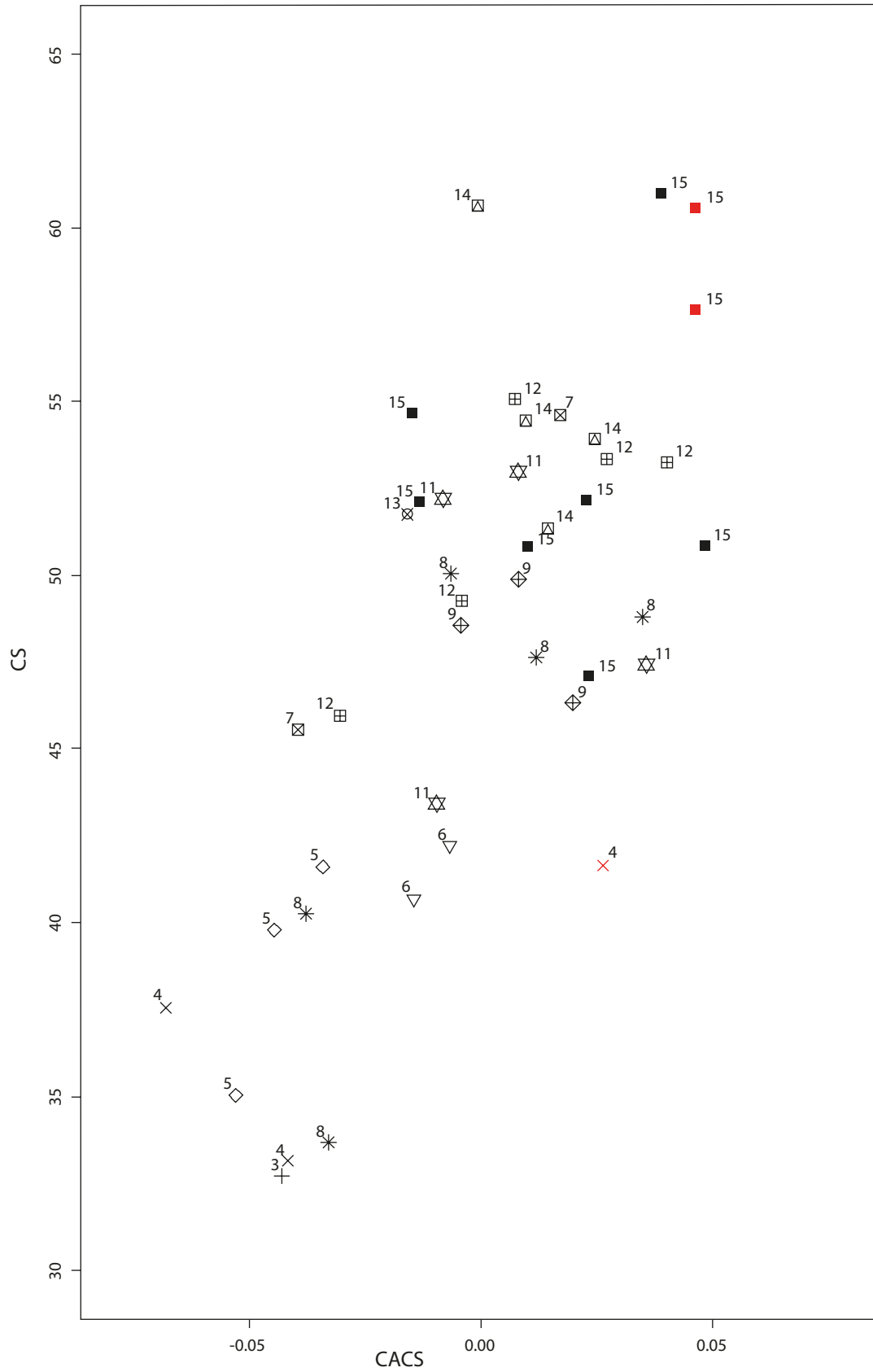


FIG. 8. — Common Allometric Component scores (CACs) versus Centroid Size (CS). Species: **black points**, *Hippopotamus amphibius* Linnaeus, 1758; **red points**, *Hippopotamus gorgops* Dietrich, 1928. Numbers on plotted points refer to class ages (see Methods). **Plus**, class 3; **cross**, class 4; **diamond**, class 5; **triangle point down**, class 6; **square cross**, class 7; **star**, class 8; **diamond plus**, class 9; **triangles up and down**, class 11; **square plus**, class 12; **square and triangle**, class 14; **filled square**, class 15.

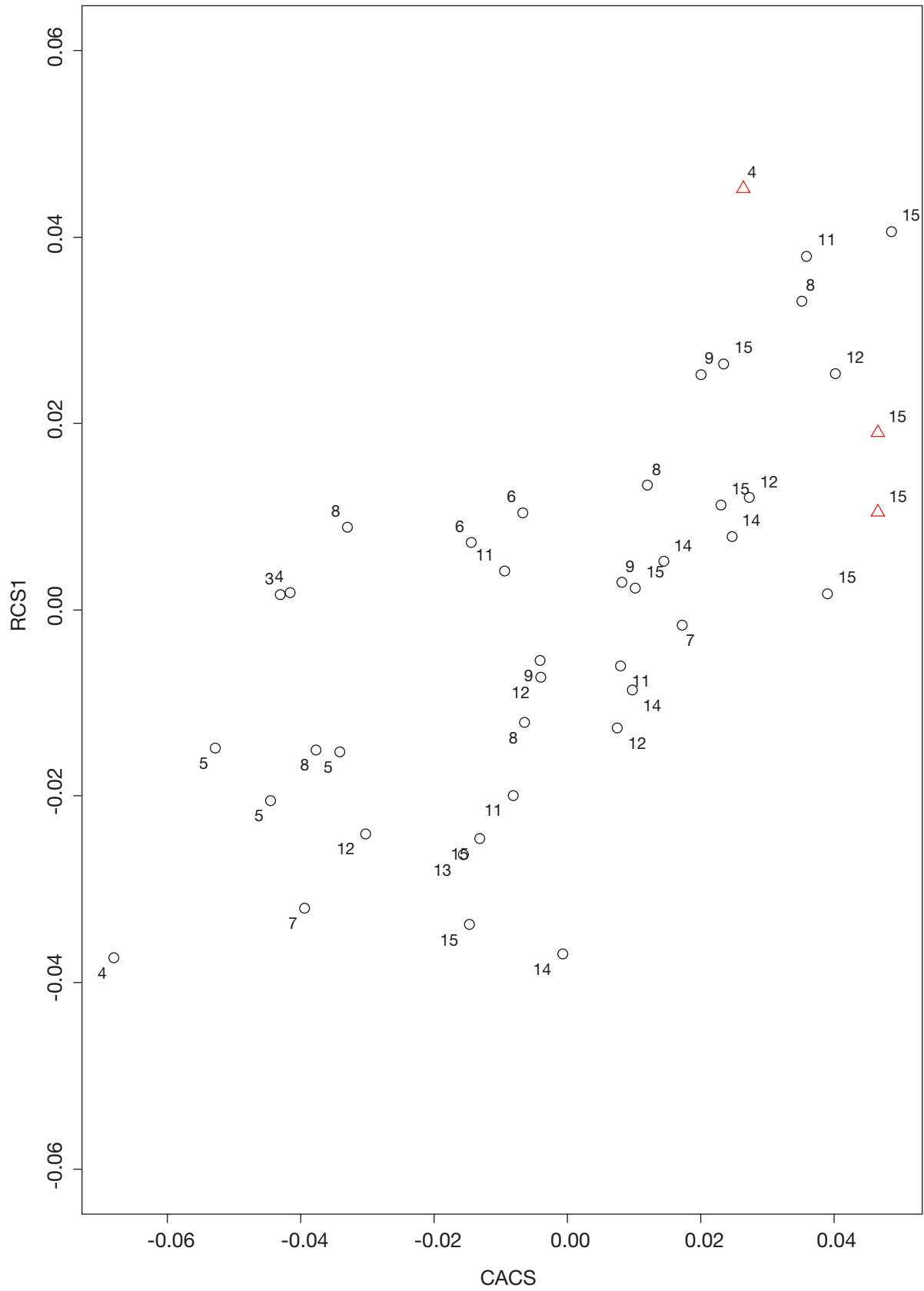


FIG. 9. — Common Allometric Component scores (CACs) versus first residual shape component (RCS1). Species: **circle**, *Hippopotamus amphibius* Linnaeus, 1758; **triangle**, *Hippopotamus gorgops* Dietrich, 1928. Numbers on plotted points refer to class ages (see Methods).

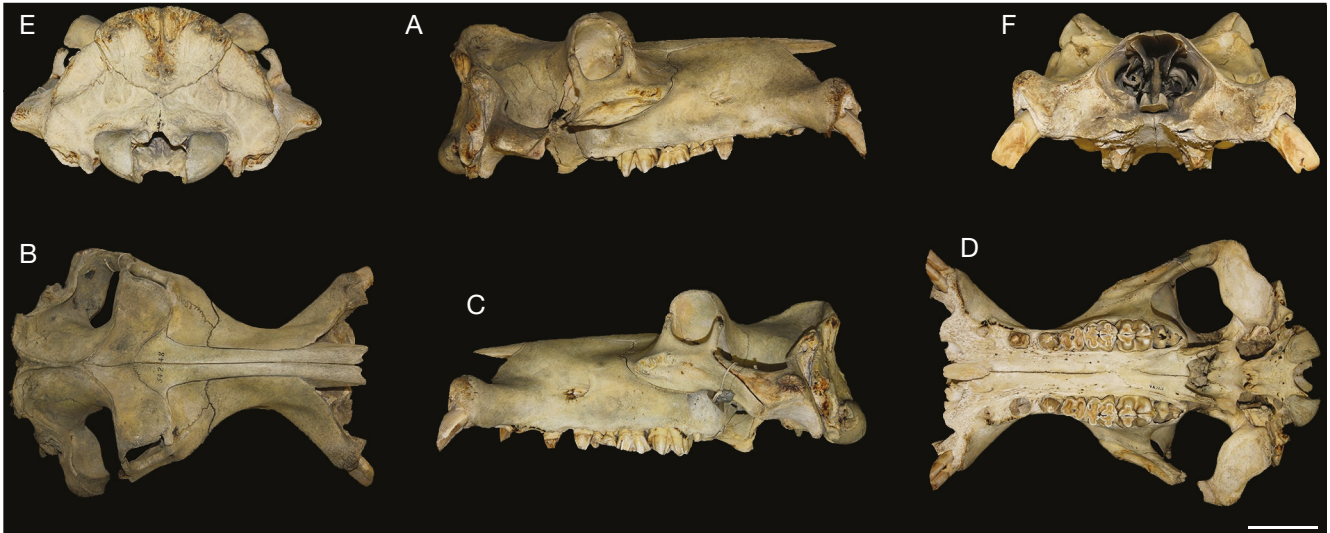


FIG. 10. — Cranium AMNH 54248, juvenile specimen of *Hippopotamus amphibius* Linnaeus, 1758 (housed at the American Museum of Natural History, New York): **A**, right lateral view; **B**, upper view; **C**, left lateral view; **D**, lower view; **E**, posterior view; **F**, anterior view. Scale bar: 10 cm.

towards a better understanding of ontogenetic shape variations in fossil hippopotamids by means of GM data. The results obtained for *Hip. amphibius* reveal a strict correlation between size and shape, that needs a more detailed investigation. The ontogenetic variations here detected in *Hip. amphibius*, were not highlighted by van der Geer *et al.* (2018). They focused on island hippopotamuses, using a different landmark configuration, excluding the top of the orbit and the nuchal crest. Nevertheless, van der Geer *et al.* (2018) recognized anatomical variations during the ontogenetic stages in the *Hip. amphibius* skull shape, characterized by elongation of the nasal bones and the palate (not much detected here because the rostral area of the cranium has been excluded from the landmark configuration; see Material and Methods) which also become high and wide. Other researchers investigated allometric growth of extant hippopotamuses basing on linear measurements and traditional morphometrics (e.g. Weston 2003) suggesting the neurocranium becomes smaller as the hippopotamus grow while the rostral area becomes larger; nevertheless, most of allometric changes were detected in the mandible (Weston 2003).

Hippopotamus gorgops displays more advanced anatomical features than its extant relative *Hip. amphibius* (i.e., very elevated orbits, high occipital crest, shortened postorbital region, high-crowned molars, relatively low cingula, splayed roots on the upper molars: Coryndon 1970a, 1970b; Harris 1991; Weston & Boisserie 2010). This adaptation is more developed in the advanced forms of this fossil species (Coryndon 1970a, 1970b; Weston & Boisserie 2010), having an extremely derived anatomy probably related to a more specialized aquatic behavior rather than the more conservative extant amphibious form. This general morphology is well recorded in the adult individuals of this giant hippo species, which are very abundant in the Buia assemblage. Such a derived anatomy is characterized by: 1) the extremely elevated orbits; 2) nuchal and sagittal crests; and

3) the elongation of the nasal bones and the palate. This set of characteristics is present in the juvenile specimen from Buia and less marked in the juvenile sample individuals of *Hip. amphibius* (compare Figure 4 with Figure 10). Skulls of *Hip. amphibius* and *Hip. gorgops* at the same ontogenetic stage (i.e., class ages 4, juveniles, and 15, adults) are indeed plott well-separated of the GM morphospace (Figs 5; 6) displaying well defined shapes in lateral view and for the considered configuration. Of course, the discovery of much more well-preserved skulls of *Hip. gorgops*, in particular juvenile specimens, would be useful to investigate more details of the ontogenetic trajectories in this species. The postcranial bones of *Hip. gorgops* still are large in size and stoutly built (see Martínez-Navarro *et al.* 2004b) showing that with its fully developed and strong limbs, the individuals of this species were able to move well on land, like the extant *Hip. amphibius*. In any case, the interpretation of the differences in cranial anatomy of *Hip. gorgops* in respect to *Hip. amphibius*, may suggest that the derived cranial morphology on the first is reflecting a different way of living in water but, most probably, it is related to a more water-adapted lifestyle (see also Coryndon 1977).

In Europe, the almost coeval and probably closest relative species to *Hip. gorgops*, *Hip. antiquus*, shows marked similarities in the cranial morphology suggesting a similar life style (Stuenes 1989; Martínez-Navarro *et al.* 2015; Pandolfi *et al.* 2020). Also, a study of a biogeochemical sample from the assemblage of the Early Pleistocene site of Venta Micena (southern Spain) has demonstrated that the concentration of $\delta^{15}\text{N}$ in the bones of *Hip. antiquus* was extremely high, suggesting that this species did not eat terrestrial plants and was limiting its alimentary income within aquatic plants only, since the latter do not fix the atmospheric N_2 . These results are consistent with the interpretation of more specialized aquatic lifestyle of this European hippo (Palmqvist *et al.* 2003; Martínez-Navarro *et al.* 2004a, 2015).

Because of the similar anatomy between the European *Hip. antiquus* and the African forms *Hip. gorgops* (juveniles and adults), it is suggested here that both species were probably more specialized in their aquatic habits than the extant *Hip. amphibius*.

CONCLUSIONS

The paleoanthropological site of Buia has yielded one of the best late Early Pleistocene fossil records in East Africa. The members of the family Hippopotamidae are common and abundant animals in Plio-Pleistocene archaeological sites and at Buia they are the dominant megaherbivores within the mammalian assemblages, where are represented by two co-occurring species: *Hippopotamus gorgops* and aff. *Hippopotamus* sp. (small size).

The juvenile cranial specimen of *Hip. gorgops* described here shows a highly derived cranial anatomy, with elevated nuchal and sagittal crests, very elevated orbital cavities, short neurocranium, elongated zygomatic arches, and an elongated muzzle. This anatomy is similar to that of the adult giants forms of *Hip. gorgops*, showing the diagnostic characters of the species evident since an early ontogenetic stage. The functional interpretation of such cranial anatomy is probably related as a response to an extreme specialization to an aquatic habitat, at a much higher degree than both extant and fossil species of this evolutionary lineage.

Acknowledgements

The Buia Project research activities have been possible thanks to the financial support of several funding institutions: the University of Florence, the Italian Ministry for Foreign Affairs (MAECI, DGSP-VI), the Italian Ministry for Education and Research (projects leaders E. Abbate [PRIN2001045397 and PRIN2005049192] and M. Ghinassi. [PRIN2012MY8AB2]), the Leakey Foundation (2000, 2001, 2003 grants to LR), the National Geographic Society (7949-05 to LR), the Spanish Ministry of Economy and Competitiveness (grant CGL2016-80975-P to BMN), the Generalitat de Catalunya, Spain, (grant GENCAT 2017SGR 859 to BMN) and the Palarq Foundation, Barcelona, Spain (to BMN and TM). We also thank J.-R. Boisserie for his advices in the interpretation of the anatomy of the specimen. The preparation of cranial remains has been carried out with long patient work in the National Museum of Asmara by LR and BMN with the precious help and assistance of F. Cozzini, F. Landucci, and A. Segid. We also thank the American Museum of Natural History, New York, for access to the osteological collections. S. Almécija, J. Madurell-Malapeira and S. Ros-Montoya helped with the photographs and preparation of the Figures 4 and 10. LP is granted by University of Florence (“Progetto Giovani Ricercatori Protagonisti” initiative; research project “Ecomorphology of fossil and extant Hippopotamids and Rhinocerotids”); LP thanks the European Commission’s Research Infrastructure Action, EU-SYNTHESYS+ project

BE-TAF-1367; part of this research received support from the SYNTHESYS+ Project <http://www.synthesys.info/> which is funded by the European Commission. We thank Elena Arbolino for the drawing of the hippo’s skull in figure 3. Florent Rivals did the French translation of the abstract and the title. A final mention to the entire staff of the National Museum of Eritrea and the Eritrean Commission of Culture and Sports (Asmara) for continuous support offered to the Project, and to the people of the Buia village for warm hospitality and friendship granted to the “Buia Project” since 1995. Finally, we thank the associate editor R. Macchiarelli and two anonymous reviewers for their useful comments and suggestions.

REFERENCES

- ABBATE E., ALBIANELLI A., AZZAROLI A., BENVENUTI M., TESFAMARIAM B., BRUNI P., CIPRIANI N., CLARKE R. J., FICCARELLI G., MACCHIARELLI R., NAPOLEONE G., PAPINI M., ROOK L., SAGRI M., TECLÉ T. M., TORRE D., & VILLA I. 1998. — A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea. *Nature* 393: 458-460. <https://doi.org/10.1038/30954>
- ABBATE E., WOLDEHAIMANOT B., LIBSEKAL Y., TECLÉ T. M. & ROOK L. 2004a. — A step towards human origins: The Buia *Homo* one-million-years ago in the Eritrean Danakil Depression (East Africa). *Rivista Italiana di Paleontologia e Stratigrafia* 110: 1-144.
- ABBATE E., WOLDEHAIMANOT B., BRUNI P., FALORNI P., PAPINI M., SAGRI M., GRMAY S. & TECLÉ T. M. 2004b. — Geology of the *Homo*-bearing Pleistocene Dandiero Basin (Buia Region; Eritrea Danakil Depression). *Rivista Italiana di Stratigrafia e Paleontologia* 110: 5-34.
- ALBIANELLI A. & NAPOLEONE G. 2004. — Magnetostratigraphy of the *Homo*-bearing Pleistocene Dandiero Basin (Danakil Depression, Eritrea). *Rivista Italiana di Stratigrafia e Paleontologia* 110: 35-44.
- ARISTIDE L., STRAUSS A., HALENAR-PRICE L. B., GILISSEN E., CRUZ F. W., CARTELLE C., ROSENBERG A. L., LOPES R. T., DOS REIS S. F. & IVAN PEREZ S. 2019. — Cranial and endocranial diversity in extant and fossil atelids (Platyrrhini: Atelidae): A geometric morphometric study. *American Journal of Physical Anthropology*: 1-10. <https://doi.org/10.1002/ajpa.23837>
- BIGAZZI G., BALESTRIERI M. L., NORELLI P. & ODDONE M. 2004. — Fission-track dating of a tephra layer in the Alat formation of the Dandiero Group (Danakil Depression, Eritrea). *Rivista Italiana di Stratigrafia e Paleontologia* 110: 45-49.
- BOISSERIE J.-R. 2002. — *Nouveaux Hippopotamidae du Mio-Pliocène du Tchad et d’Ethiopie: implications phylogénétiques et paléoenvironnementales*. PhD dissertation, Université de Poitiers, Poitiers, 440 p.
- BOISSERIE J.-R. 2005. — The phylogeny and taxonomy of Hippopotamidae (Mammalia, Artiodactyla): a review based on morphology and cladistic analysis. *Zoological Journal of the Linnean Society* 143: 1-26. <https://doi.org/10.1111/j.1096-3642.2004.00138.x>
- BOISSERIE J.-R. 2007. — Family Hippopotamidae, in PROTHERO D. R. & FOSS S. E. (eds), *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore: 106-119.
- BOOKSTEIN F. L. 1986. — Size and shape spaces for landmark data in two dimensions. *Statistical Science* 1 (2): 181-222. <https://doi.org/10.1214/ss/1177013696>
- BOOKSTEIN F. L. 1991. — *Morphometric tools for landmark data*. Cambridge University Press, Cambridge, 435 p. <https://doi.org/10.1017/CBO9780511573064>
- BOISSERIE J.-R. & WHITE T. D. 2004. — A new species of Pliocene Hippopotamidae from the Middle Awash, Ethiopia. *Journal of Vertebrate Paleontology* 24 (2): 464-473. <https://doi.org/10.1671/2475>

- BOISSERIE J.-R., LIKIUS A., VIGNAUD P. & BRUNET M. 2005. — A new late Miocene hippopotamid from Toros-Ménalla, Chad. *Journal of Vertebrate Paleontology* 25: 665-673. <https://doi.org/10.1666/03-077>
- BRIDGE J. S. 2003. — *Rivers and Floodplains*. Blackwell Scientific Publications, Oxford, 491p. <https://doi.org/10.1002/jqs.856>
- CORYNDON S. C. 1970a. — Evolutionary trends in East African Hippopotamidae. *Bulletin de Liaison de l'Association Sénégalaise pour l'Étude du Quaternaire de l'Ouest africain (AS ÉQUA)*, Dakar 25: 107-116.
- CORYNDON S. C. 1970b. — The extent of variation in fossil *Hippopotamus* from Africa. *Symposia of the Zoological Society of London* 26: 135-147.
- CORYNDON S. C. 1976. — Fossil Hippopotamidae from Plio-Pleistocene successions of the Rudolf Basin, in COPPENS Y., HOWELL F. C., ISAAC G. L. & LEAKEY R. E. F. (eds), *Earliest man and environments in the Lake Rudolf Basin*. University of Chicago Press, Chicago: 238-250.
- CORYNDON S. C. 1977. — Hippopotamidae, in MAGLIO V. J. & COOKE H. B. S. (eds), *Evolution of African Mammals*. Harvard University Press, Cambridge, United States: 483-495.
- DELFINO M., SEGID A., YOSIEF D., SHOSHANI J., ROOK L. & LIBSEKAL Y. 2004. — Fossil reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). *Rivista Italiana di Paleontologia e Stratigrafia* 110: 51-60.
- DELFINO M., CANDILIO F., CARNEVALE G., COPPA A., MEDIN T., PAVIA M., ROOK L., URCIUOLI A. & VILLA A. 2018. — The early Pleistocene vertebrate fauna of Mulhuli-Amo (Buia area, Danakil Depression, Eritrea). *Bollettino della Società Paleontologica Italiana* 57: 27-44.
- DIETRICH W. O. 1926. — Fortschritte der Säugetierpaläontologie Afrikas. *Forschungen und Fortschritte* 15: 121-122.
- DIETRICH W. O. 1928. — Pleistocene Deutsch-Ostafrikanische *Hippopotamus*-reste. *Wissenschaftliche Ergebnisse des Oldoway Expedition Herausgeben Von Prof. Dr. Reck* 3: 3-41.
- FAURE M. 1986. — Les Hippopotamidés du Pléistocène ancien d'Oubeidyeh (Israël), in TCHERNOV E. (ed.), *Les Mammifères du Pléistocène inférieur de la Vallée du Jourdain à Oubeidyeh*. (Vol. 5). Paris : Mémoires et Travaux du Centre de Recherche Français de Jérusalem. Association Paleorient, Paris: 107-142
- FAURE M. 1994. — Les Hippopotamidae (Mammalia, Artiodactyla) du rift occidental (bassin du lac Albert, Ouganda). Etude Préliminaire, in: SENUT B. & PICKFORD M. (eds), *Geology and paleobiology of the Albertine Rift Valley, Uganda-Zaire, II: paleobiology*. CI FEG, Orléans: 321-337.
- FERRETTI M. P., FICCARELLI G., LIBSEKAL Y., TECLÉ T. M. & ROOK L. 2003. — Fossil elephants from Buia (northern Afar Depression, Eritrea) with remarks on the Systematics of *Elephas recki* (Proboscidea, Elephantidae). *Journal of Vertebrate Paleontology* 23 (1): 244-257. <https://doi.org/10.1666/03-077>
- FIDOLINI F., GHINASSI M., ALDINUCCI M., BILLI P., BOAGA J., DEIANA R. & BRIVIO L. 2013. — Fault-sourced alluvial fans and their interaction with axial fluvial drainage: an example from the Plio-Pleistocene Upper Valdarno Basin (Tuscany, Italy). *Sedimentary Geology* 289: 19-39. <https://doi.org/10.1016/j.sedgeo.2013.02.004>
- GÉZE R. 1980. — *Les Hippopotamidae (Mammalia, Artiodactyla) du Plio-Pléistocène de l'Éthiopie (Afrique orientale)*. PhD dissertation, Université Pierre et Marie Curie-Paris VI, Paris, 116 p.
- GÉZE R. 1985. — Répartition paléocologique et relations phylogénétiques des Hippopotamidae (Mammalia, Artiodactyla) du Néogène d'Afrique Orientale, in COPPENS Y. (ed.), *L'Environnement des Hominiés au Plio-Pléistocène*. Masson, Paris: 81-100.
- GHINASSI M., ABBAZZI L., ESU D., GAUDANT J. & GIROTTI O. 2005. — Facies analysis, stratigraphy and palaeontology (molluscs and vertebrates) in the Upper Pliocene sandy flood-basin deposits of the Upper Valdarno Basin (Northern Apennines). *Rivista Italiana di Paleontologia e Stratigrafia* 111 (3): 467-487. <https://doi.org/10.13130/2039-4942/6332>
- GHINASSI G., PAPINI M., LIBSEKAL Y. & ROOK L. 2009. — Palaeoenvironments of the Buia *Homo* site: high-resolution facies analysis and non-marine sequence stratigraphy in the Alat formation (Pleistocene Dandiero Basin, Danakil depression, Eritrea). *Palaeogeography, Palaeoclimatology, Palaeoecology* 280 (3-4): 415-431. <https://doi.org/10.1016/j.palaeo.2009.06.029>
- GHINASSI M., BILLI P., LIBSEKAL Y., PAPINI M. & ROOK L. 2013. — Inferring fluvial morphodynamics and overbank flow control from 3D outcrop sections of a Pleistocene point bar, Dandiero Basin, Eritrea. *Journal of Sedimentary Research* 83: 1065-1083. <https://doi.org/10.2110/jsr.2013.80>
- GHINASSI M., OMS O., PAPINI M., SCARCIGLIA F., CARNEVALE G., SANI F., ROOK L., DELFINO M., PAVIA M., LIBSEKAL Y., BONDIOLI L., COPPA C., FRAYER D. & MACCHIARELLI R. 2015. — An integrated study of the *Homo*-bearing Alat stratigraphic section (Eritrea): an expanded continental record at the Early-Middle Pleistocene transition. *Journal of African Earth Sciences* 112 Part A: 163-185. <https://doi.org/10.1016/j.jafrearsci.2015.09.012>
- GOODALL C. 1991. — Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society Series B (Methodological)* 53 (2): 285-339. <https://doi.org/10.1111/j.2517-6161.1991.tb01825.x>
- HARRIS J. M., BROWN F. H. & LEAKEY M. G. 1988. — Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Sciences* 399: 1-128. <https://doi.org/10.5962/p.241284>
- HARRIS J. M. 1991. — Family Hippopotamidae, in HARRIS J. M. (ed), *Koobi Fora Research Project, The Fossil Artiodactyls, and paleoenvironments*. Vol. 3. Clarendon Press-Oxford: 31-85.
- HOOIJER D. A. 1958. — Pleistocene remains of hippopotamus from the Orange Free State. *Navorsing van die Nasionale Museum Bloemfontein* 1: 259-266.
- KENT P. E. 1942. — The Pleistocene beds of Kanam and Kanjera, Kavirondo, Kenya. *Geological Magazine* 79: 117-132. <https://doi.org/10.1017/S001675680007360X>
- LAWS R. M. 1968. — Dentition and ageing of *Hippopotamus*. *East African Wildlife Journal* 6 (1): 19-52. <https://doi.org/10.1111/j.1365-2028.1968.tb00899.x>
- MARCUS L. F., HINGST-ZAHER E. & ZAHER H. 2000. — Application of landmarks morphometrics to skull representing the orders of living mammals. *Hystrix* 11: 27-47. <https://doi.org/10.4404/hystrix-11.1-4135>
- MÁRQUEZ E. J., CABEEN R., WOODS R. P. & HOULE D. 2012. — The measurement of local variation in shape. *Evolutionary Biology* 39:419-439. <https://doi.org/10.1007/s11692-012-9159-6>
- MARTÍNEZ-NAVARRO B., PALMQVIST P., MADURELL J. & PÉREZ-CLAROS J. A. 2004a. — El registro de *Hippopotamus antiquus* en el Pleistoceno inferior de Europa: implicaciones paleoambientales e inferencias paleobiológicas. Abstracts of the XX Jornadas de Paleontología, Alcalá de Henares (Madrid): 121-122.
- MARTÍNEZ-NAVARRO B., ROOK L., SEGID A., YOSIEPH D., FERRETTI M. P., SHOSHANI J., TECLÉ T. M. & LIBSEKAL Y. 2004b. — The Large Fossil Mammals from Buia (Eritrea): Systematics, Biochronology and Palaeoenvironments. *Rivista Italiana di Paleontologia e Stratigrafia* 110: 61-88.
- MARTÍNEZ-NAVARRO B., ROOK L., PAPINI M. & LIBSEKAL Y. 2010. — A new species of bull from the Early Pleistocene paleoanthropological site of Buia (Eritrea): Parallelism on the dispersal of the genus *Bos* and the Acheulian culture. *Quaternary International* 212 (2): 169-175. <https://doi.org/10.1016/j.quaint.2009.09.003>
- MARTÍNEZ-NAVARRO B., MADURELL-MALAPEIRA J., ROS-MONTOYA S., ESPIGARES M. P., FIGUEIRIDO B., GUERRA-MERCHÁN A. & PALMQVIST P. 2015. — *Sobre la paleobiología de Hippopotamus antiquus Desmarest 1822: ¿Un megaherbívoro acuático sin análogos vivientes?*, in REOLID M. (ed.), Libro de Resúmenes XX XI Jornadas de Paleontología, Baeza: 180-182.
- MARTINI F., LIBSEKAL Y., FILIPPI O., KIROS A., MARTINO G., SEGID A., TEKA Z., YOSIEF D. & YAMANE S. 2004. — Characterization of

- lithic complexes of the Buia Basin. *Rivista Italiana di Paleontologia e Stratigrafia* 110: 99-132.
- MAZZA P. 1991. — Interrelation between Pleistocene hippopotami of Europe and Africa. *Bollettino della Società Paleontologica Italiana* 30: 153-186.
- MEDIN T., MARTÍNEZ-NAVARRO B., RIVALS F., LIBSEKAL Y. & ROOK L. 2015. — The late Early Pleistocene suid remains from the Paleoanthropological site of Buia (Eritrea): Systematics, biochronology and eco-geographical context. *Palaeogeography, Palaeoclimatology, Palaeoecology* 431: 26-42. <https://doi.org/10.1016/j.palaeo.2015.04.020>
- MITTEROECKER P., GUNZ P., BERNHARD M., SCHAEFER K. & BOOKSTEIN F. L. 2004. — Comparison of cranial ontogenetic trajectories among great apes and humans. *Journal of Human Evolution* 46: 679-698. <https://doi.org/10.1016/j.jhevol.2004.03.006>
- MULLIN S. K. & TAYLOR P. J. 2002. — The effects of parallax on geometric morphometric data. *Computers in Biology and Medicine* 32 (6): 455-464. [https://doi.org/10.1016/S0010-4825\(02\)00037-9](https://doi.org/10.1016/S0010-4825(02)00037-9)
- PALMQVIST P., GRÖCKE D. R., ARRIBAS A. & FARIÑA R. 2003. — Paleoeological reconstruction of a lower Pleistocene large mammals community using biogeochemical ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, Sr:Zn) and ecomorphological approaches. *Paleobiology* 29: 205-229. <https://doi.org/chvtz6>
- PALMQVIST P., PÉREZ-CLAROS J. A., JANIS C. M., FIGUEIRIDO B., TORREGROSA V. & GRÖCKE D. R. 2008. — Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. *Palaios* 23 (11): 724-737. <https://doi.org/10.2110/palo.2007.p07-073r>
- PANDOLFI L. & PETRONIO C. 2015. — A brief review of the occurrences of Pleistocene *Hippopotamus* (Mammalia, Hippopotamidae) in Italy. *Geologica Croatica* 68 (3): 313-319. <http://hdl.handle.net/2158/1200153>
- PANDOLFI L., MARTINO R., ROOK L. & PIRAS P. 2020. — Investigating ecological and phylogenetic constraints in Hippopotamidae skull shape. *Rivista Italiana di Paleontologia e Stratigrafia* 126: 37-49.
- PAPINI M., GHINASSI M., LIBSEKAL Y. & ROOK L. 2014. — Facies associations of the northern Dandiero Basin (Danakil depression, Eritrea, including the Pleistocene Buia *Homo* site). *Journal of Maps* 10 (1): 126-135. <https://doi.org/10.1080/17445647.2013.862748>
- REIMANN C. K. & STRAUCH F. 2008. — Ein Hippopotamus-Schädel aus dem Pliozän von Elis (Peloponnes, Griechenland). *Neues Jahrbuch für Geologie und Paläontologie* 249:203-222.
- ROHLF F. J. 2013. — tpsDI G, version 2.17. SU NY Stonybrook.
- ROOK L., GHINASSI M., CARNEVALE G., DELFINO M., PAVIA M., BONDIOLI L., CANDILIO E., COPPA A., MARTÍNEZ-NAVARRO B., MEDIN T., PAPINI M., ZANOLLI C. & LIBSEKAL Y. 2013. — Stratigraphic context and paleoenvironmental significance of minor taxa (Pisces, Reptilia, Aves, Rodentia) from the late Early Pleistocene paleoanthropological site of Buia (Eritrea). *Journal of Human Evolution* 64 (1): 83-92. <https://doi.org/10.1016/j.jhevol.2012.10.005>
- ROOK L., GHINASSI M., LIBSEKAL Y., MEDIN T., MARTÍNEZ-NAVARRO B. & PAPINI M. 2010. — Stratigraphic context and taxonomic assignment of the large cercopithecoïd (Primates, Mammalia) from the late early Pleistocene palaeoanthropological site of Buia (Eritrea). *Journal of Human Evolution* 59 (6): 692-607. <https://doi.org/10.1016/j.jhevol.2010.07.018>
- ROOK L., KIBREAB A., RUSSOM R., TECLE T. M. & ABBATE E. 2002. — The Buia Project: a collaborative geo-paleontological and paleoanthropological research project in Eritrea. *Journal of Human Evolution* 42 (3): A29-A30.
- SANI F., GHINASSI M., PAPINI M., OMS O. & FINOTELLO A. 2017. — Evolution of the northern tip of Afar triangle: inferences from the Quaternary succession of the Dandiero – Massawa area (Eritrea). *Tectonophysics* 717: 339-357. <https://doi.org/10.1016/j.tecto.2017.08.026>
- SCARCIGLIA F., MERCATANTE G., FONDEVILLA V., ANADÓN P., OMS O., DONATO P., AGNINI C., PAPINI M., ROOK L. & GHINASSI M. 2018. — Pleistocene paleosol development and paleoenvironmental dynamics in East Africa: a multiproxy record from the *Homo*-bearing Aalat pedostratigraphic succession, Dandiero Basin (Eritrea). *Quaternary Science Reviews* 191: 275-298. <https://doi.org/10.1016/j.quascirev.2018.05.015>
- SCHLAGER S. 2014. — Morpho: Calculations and visualisations related to Geometric Morphometrics. R-package version 2.0. 3-1.
- STUENES S. 1989. — Taxonomy, habits, and relationships of the subfossil Madagascan hippopotami *Hippopotamus lemerlei* and *H. madagascariensis*. *Journal of Vertebrate Paleontology* 9 (3): 241-268. <https://doi.org/10.1080/02724634.1989.10011761>
- VAN DER GEER A. A. E., LYRAS G. A., MITTEROECKER P. & MACPHEE R. D. 2018. — From Jumbo to Dumbo: Cranial Shape changes in elephants and hippos during phyletic dwarfing. *Evolutionary Biology* 45 (3): 303-317. <https://doi.org/10.1007/s11692-018-9451-1>
- ZANOLLI C., BONDIOLI L., COPPA A., DEAN C. M., BAYLE P., CANDILIO E., CAPUANI S., DREOSSI D., FIORE I., FRAYER D. W., LIBSEKAL Y., MANCINI L., ROOK L., MEDIN T. T., TUNIZ C. & MACCHIARELLI R. 2014. — The late Early Pleistocene human dental remains from Uadi Aalad and Mulhuli-Amo (Buia), Eritrean Danakil: Macromorphology and microstructure. *Journal of Human Evolution* 74: 96-113. <https://doi.org/10.1016/j.jhevol.2014.04.005>
- WESTON E. M. 2003. — Evolution of ontogeny in the hippopotamus skull: using allometry to dissect developmental change. *Biological Journal of the Linnean Society* 80 (4): 625-638. <https://doi.org/10.1111/j.1095-8312.2003.00263.x>
- WESTON E. & BOISSERIE J.-R. 2010. — Hippopotamidae, in WERDELIN L. & SANDERS W. J. (eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley (CA): 853-871.
- WILLIS B. J. & BEHRENSMEYER A. K. 1994. — Architecture of Miocene Overbank Deposits in Northern Pakistan. *Journal of Sedimentary Research* B64 (1): 60-67.

*Submitted on 22 January 2020;
accepted on 8 August 2020;
published on 22 February 2022.*

APPENDICES

APPENDIX 1. — List of specimens considered in the cranial shape analyses with their repository, relative ages, PC scores and Centroid Size values (see text): https://doi.org/10.5852/cr-palevol2022v21a7_s1

APPENDIX 2. — Estimated class-ages of considered *Hippopotamus* Linnaeus, 1758 specimens basing on the tooth-wear pattern: https://doi.org/10.5852/cr-palevol2022v21a7_s2

APPENDIX 3. — Animated 3D-plot of PC1, PC2 and PC3 of the considered *Hippopotamus* Linnaeus, 1758 skulls in lateral view. **Red points**, *Hippopotamus gorgops* Dietrich, 1928, **black points**, *Hippopotamus amphibius* Linnaeus, 1758. Numbers on plotted points and symbols refer to relative ontogenetic stage (see Methods and Appendices): https://doi.org/10.5852/cr-palevol2022v21a7_s3